Historical Reconstruction, Through Qualitative Modeling, Of The Effects Of Exotic Fish Introductions In Tenmile Lakes Oregon

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Abstract- *A general overview of qualitative modeling is presented in the context of fisheries management. A historic reconstruction of exotic fish introductions to Tenmile Lakes was qualitatively modeled based on foodwebs drawn from diet studies of the system. The history of species introductions in Tenmile Lakes can be characterized as one that has driven the system into neutral responses and neutral stability, with correlations between native species being inverted, certain species loosing their ability to respond to system input, and an overall loss of opportunity for management options. Expected outcomes to predator-prey interactions were not supported by model predictions, due to indirect effects from complex interactions between the mix of native and introduced species. The use of exotic fish predators to control undesirable species was predicted to have an effect that was opposite to management objectives. In its present state the system, as modeled, defies predictable management.*

Introduction

> "...he will learn little if he limits himself to that species. He must evidently study also the species upon which it depends for its existence, and the various conditions upon which *these* depend. He must likewise study the species with which it comes in competition, and the entire system of conditions affecting their prosperity." (Forbes 1887)

In 1887, Steven A. Forbes laid out in unmatched prose the complexity of a lake environment, and the imperative to study the entire "microcosm" presented by biological systems, both in terms of the context of their physical environment, and in terms of the interactions between species in the community. It remains today an enormous challenge. While the ecosystem has long been defined as a unit of study (Tansley 1935), its arrival into management and ecological research has only been recently emphasized (McIntosh 1985). And while the need to research and manage whole communities and ecosystems rather than just single species, has been recognized, working notions of how to accomplish this daunting task have been vague. Biologist striving to gain understanding of complex biological systems, inevitably turn to models of the world as a means for organizing their hypotheses and approaches.

Modeling approaches

Levins (1966) ascribes three properties to all models: 1) *generality*, 2) *realism*, and 3) *precision*. For a model to be manageable only two of these can be maximized in a given application; to emphasize all three would require the impossible task of duplicating nature. The critical decision then, is to decide which property to sacrifice for the other two. Models that sacrifice generality for realism and precision can be described as *Mechanistic models*, they are commonly applied by natural resource managers, especially in fisheries (e.g. stock recruitment and yield models, bioenergetic models). Intensive data collection and comprehensive equations yield precise and testable predictions, but applications are restricted by a narrow range of initial conditions. *Statistical models*, which sacrifice realism, are useful for describing general patterns with measured confidence, but correlations are not transferable into causalities, and one is left with little understanding of the workings of the real world. *Qualitative models* sacrifice precision in favor of generality and realism. They are free from the constraints of extensive and expensive data collection, and while their predictions are only qualitative (i.e. only the direction of change in a system, and not the absolute amount, is predicted), they are nonetheless rigorous in their derivation, and produce testable hypotheses. Levins (1974, 1975; Puccia and Levins 1985) developed a method of modeling interactions among populations, termed *loop analysis*, but which is also specifically referred to as *qualitative analysis*, that is ideally suited to the study of complex biological systems with many interacting variables.

Application of qualitative modeling to management of biological communities

Qualitative modeling meets the requirement of community and ecosystem level models. It accommodates large temporal and spatial scales, is generally applicable, mathematically rigorous, and has high correspondence between model parameters and the biology of ecosystem. It has simple data requirements. Essentially the data input describes the interactions among species, in large part this is simply foodweb structure, as modified by competition, parasitism, etc.. Model outputs are used to evaluate community stability and predict ecological change, through a prediction matrix. These in turn can be used to focus research efforts on critical interactions and develop testable hypotheses of system behavior. Below we present a general overview of the qualitative modeling method, followed by an example application to the problem of introduced fish species in Tenmile Lakes, Oregon.

Overview of qualitative modeling

General Methodology

Detailed procedures for qualitative modeling are described in Puccia and Levins (1985). Li et al. (In Press) present convenient methodology for using symbolic mathematical PC based software. Qualitative models build up from the population level to the community level by way of interaction terms between populations. Implicit within these models are the Malthusian parameters of population size, birth rate, death rate, and mean generation time. Interaction terms are drawn from per capita effects within Lotka-Volterra equations (Figure 1). Qualitative analysis omits quantitative expression of these terms, and instead relies only upon which species are present, and the nature of their interactions. These relationships are generally depicted by signed digraphs (a.k.a. sign-directed graphs), which contain all of the essential information needed for qualitative modeling. Signed digraphs can be used to depict all possible relationships between species (Figure 2), in terms of trophic interactions, competitive interactions, and self-regulation. Self-regulation in the context of qualitative models stems from a species gaining resources from outside the model system. All that is used in qualitative modeling is the sign of the interaction terms for each species in a community, and together these interaction terms form the basis for the community matrix (Figure 3). The community matrix contains all the information of the signed digraph, and its analysis yields two basic products: 1) an assessment of community stability through system feedback, and 2) a prediction matrix that details the response of populations, in terms of abundance, to input to the other populations within the system. System stability is described numerically, in part, by overall system feedback (Figure 4), and can be placed in the three general categories of stable, unstable, and neutrally stable states. Prediction matrices are developed directly through algebraic manipulations of the community matrix (transpose$(-A)^{-1}$, where A is the community matrix). These predictions are essentially testable hypotheses about how the system responds to chronic (press) disturbances (Bender et al. 1984).

Model example

An example of a signed digraph and prediction matrix is presented in Figure 5, which describes a system of interacting populations of invertebrates, fish consumers, and a specialized predator that feeds exclusively on one of the fishes. The prediction matrix depicts the numerical response of populations to positive input to the system. Positive input is viewed in terms of increases to the birth rate, or decreases in the death rate of an individual population. Input to the system is read along the rows, and population responses are read down the columns. In ecological terms positive input can be in the way of fertilization to nutrient poor systems, or increased cover for a herbivore to escape from its predator, or conversely increased cover for a predator to ambush its prey. To depict increases in the death rate of a population, one merely reverses the signs of the responses in the prediction matrix. For instance, in Figure 5, increasing the production of invertebrates through an increase in their food supply (which is read along the first row) is predicted to create no change in the population size of invertebrates, an increase in Fish A, no change in Fish B, and a decrease in the predator population. Competition between the two fish consumers creates positive feedback in the system through the A-to-B-to-I-to-A loop (i.e. multiplying the signs of each interaction term (-,-,+) in this loop yields a positive term). In this instance, the positive feedback creates counterintuitive behavior in the model; an increase in the predators birth rate is predicted to create a decrease in the size of the predator population! However, such a system is not likely to exist, as overall feedback in this model is positive, which would likely create unstable population fluctuations. Although subsystems of large stable communities can contain positive feedback loops that create similarly counterintuitive behavior. Hence an essential use of qualitative modeling is to identify interactions that are critical to system behavior. And while this can be advantageous in forecasting the effects of changes in community structure or management actions, it can also be useful in understanding past system behavior, so that present management actions can be considered within a historical context.

Exotic Fish Introductions to Tenmile Lakes, Oregon

Historic reconstruction of community structure

Tenmile Lakes are an interconnected series of shallow freshwater lakes formed behind sand dunes along the southern coast of Oregon (Figure 6). The lakes are eutrophic, and have dense growths of aquatic vegetation covering soft bottom sediments of sand and silt. The native fish community of the lake system included coho salmon (*Oncorhynchus kisutch*), steelhead (*O. mykiss*), cutthroat trout (*O. clarki*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), eulachon (*Thaleichthys pacificus*), and lamprey (*Lampetra* spp.) ammocoetes. There is an extensive history of introductions of warmwater exotic fishes since the 1920's (Table 1), including yellow perch (*Perca flavescens*), brown bullhead (*Ictalurus nebulosus*), bluegill (*Lepomus macrochirus*), largemouth bass (*Micropterus salmoides*), a hybrid of striped bass (*Morone saxatilis*) x white bass (*M. chrysops*), and black crappie (*Pomoxis nigromaculatus*). All of these introductions were unauthorized except for largemouth bass and hybrid bass (ODFW 1991). During the 1940's the Tenmile Lakes watershed was logged extensively, which accelerated sedimentation in the lake and stream systems. The Brazilian waterweed (*Elodea densa*) was first noted in 1947, and quickly spread throughout the lake system, forming thick beds; other introduced macrophytes include water milfoil (*Myriophilum verticillatum*), and the water lily (*Nymphaea ordorata*). The increased sedimentation of the lake enhanced macrophyte production, which in turn created favorable conditions for the reproduction and rearing of warmwater fishes. The coho salmon population declined dramatically, and competition and predation from warmwater fish were thought to be the major cause, although habitat degradation has also been implicated. A large-scale rotenone treatment was done in 1968 to curb the effects of a superabundant population of bluegill as well as other warmwater fishes. The treatment eradicated yellow perch, but not bluegill and brown bullhead. The bluegill population rebounded immediately, and largemouth bass were introduced in 1971 for the purpose of their control, and also for the purpose of supporting recreational fisheries. Hybrid bass, which were expected to be sterile, were planted in the lake system from 1982 to 1998, for the same management goals. The program was discontinued when it was discovered that some hybrid bass had reproduced. In the mid 1980's yellow perch were apparently reintroduced illegally, however their appearance in sport catches and sampling efforts has been rare. The latest introduction was of black crappie, which were found to be widespread in the lake system in 1994.

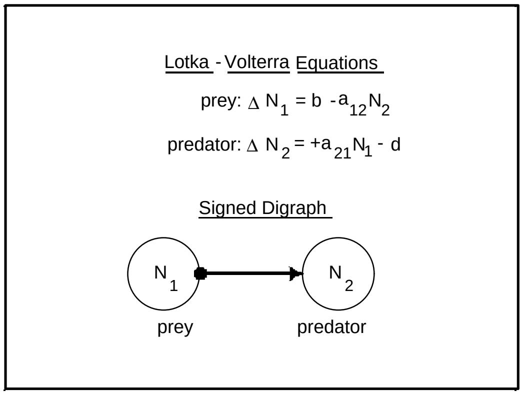


Figure 1. Lotka-Volterra equations for simple predator-prey relationship, and corresponding signed digraph; N_j: population size of species j, b: birth rate, d: death rate. Prey 1 has a positive per capita effect on predator 2, denoted by the arrow, and symbolized by the interaction term $+a_{21}$. Predator 2 has a negative per capita effect on prey 1, denoted by filled circle, and denoted by interaction term $-a_{12}$.

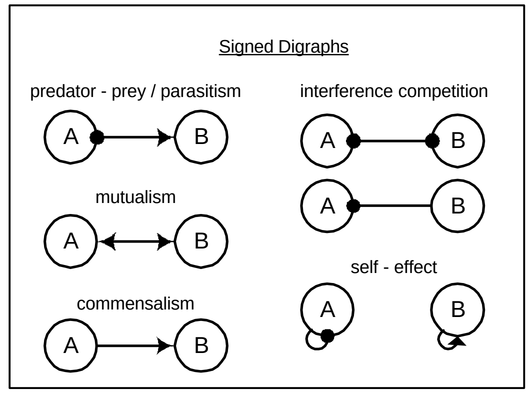


Figure 2. Signed digraphs of possible interaction pairs and self regulation for two species, A and B. Arrows denote positive feedback, filled circles negative feedback.

community matrix

$$\begin{bmatrix} 0 & -a_{12} \\ +a_{21} & 0 \end{bmatrix}$$

Figure 3. Qualitative community matrix with simple predator-prey interaction terms expressed symbolically. These terms can also be numerically expressed as -1 ($-a_{12}$) and +1 ($+a_{21}$).

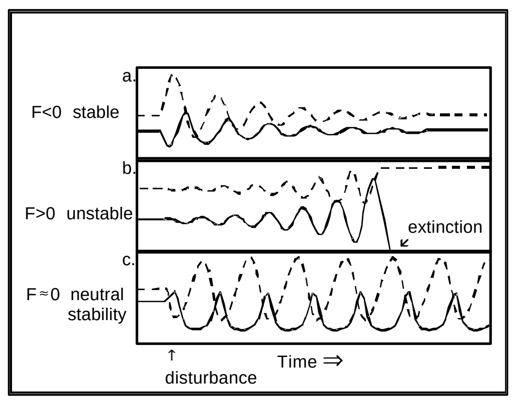
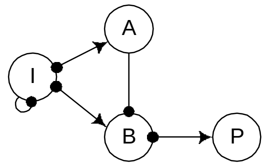


Figure 4. Generalized pattern of population fluctuations, following disturbance in communities, with (a.) overall system feedback (F)<0, creating stable dampened oscillations, with (b.) F>0, creating unstable oscillations with increasing amplitude, and with (c.) F≈ creating unregulated oscillations. Stable systems with negative feedback return to equilibrium following a disturbance. Extinctions are likely in unstable systems where overall feedback is positive. Systems that are near neutral stability tend to drift randomly with no tendency towards equilibrium conditions.



Prediction matrix

Positive input to:	Response of: Invert.	Fish A	Fish B	Pred.
Invert.	0	1	0	-1
Fish A	-1	1	0	-1
Fish B	0	0	0	1
Pred.	0	1	-1	-1

Figure 5. Prediction matrix depicting population response to system input in terms of positive (1), negative (-1), or neutral (0), changes in population abundance; Invert.: invertebrates, Pred.: predators. System inputs are in terms of increases to birth rates of model populations. In this example positive feedback in the A-to-B-to-I-to-A loop produces the counterintuitive response of a decrease in the predator population from an increase to the birth rate of predators (adapted from Puccia and Levins 1985).

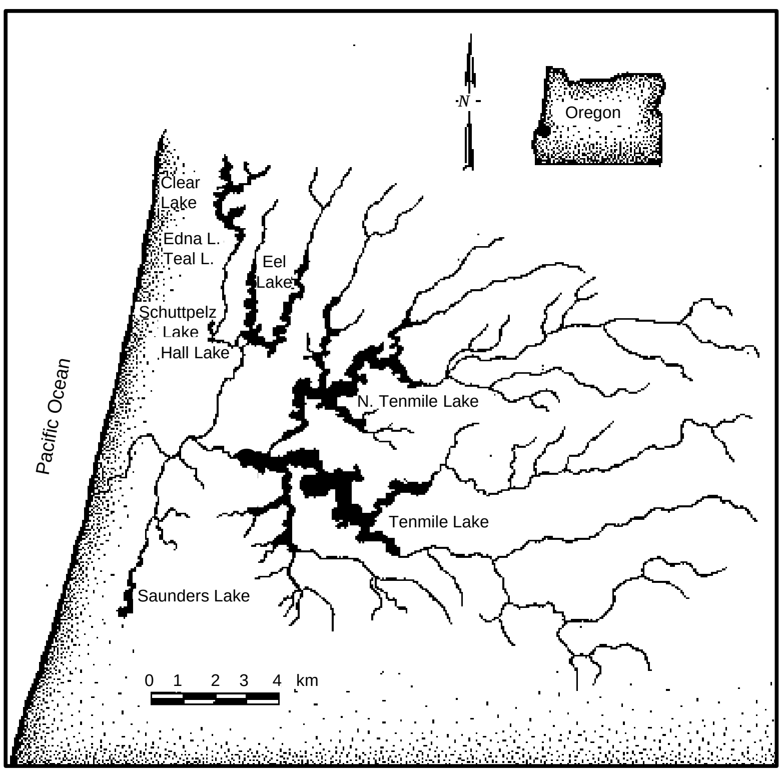


Figure 6. Map of the Tenmile Lakes basin (adapted from Gestring 1991).

Table 1. History of introductions and management in Tenmile Lakes, Oregon, and corresponding community models 1-6.

Species	1920 ⎡	1930 ⎡	1940 ⎡ ⇓[a]	⇓[b] 1950 ⎡	1960 ⎡	⇓[c] 1970 ⎡	1980 ⎡	1990 ⎡	2000 ⎡
yellow perch[d]	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxx				
brown bullhead	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	
bluegill					xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	
largemouth bass						xxxxxxxxxx	xxxxxxxxxx	xxxxxxxxxx	
hybrid bass[e]							xxxxxxx		
black crappie								xxxxxx	
Model #:	1 |	2			| 3 | 4 |		5	| 6	

[a]: 1940's-basin logged, sedimentation of lake and stream habitat.
[b]: 1947-Brazillian waterweed (*Elodea densa*) introduced, later introductions of water milfoil (*Myriophilum verticillatum*), and the water lily (*Nymphaea ordorata*).
[c]: 1968-rotenone treatment of entire lake system.
[d]: unauthorized reintroduction in the mid 1980's, population at very low levels.
[e]: hybrid of striped bass (*Morone saxatilis*) x white bass (*M. chrysops*), predominantly sterile.

To illustrate the effects that community structure has had upon management options for coho salmon in the Tenmile Lakes system, we analyzed 6 foodweb models that spanned a time series from pre-1920's to the present (Table 1). Foodweb structure was based on stomach contents sampling (1985-1990 sampling; unpublished data, Oregon Department of Fish and Wildlife), and reference texts for fish (Scott and Crossman 1973) and invertebrates (Merrit and Cummins 1984). The most important food item for fish in the system is the mysid (a.k.a. oppossum) shrimp (*Neomysis mercedis*), which during their peak abundance, can dominate the water column of the lake. The models focused on the community associated with juvenile coho salmon rearing in the lake system. Eulachon and steelhead were not included in the models, as they use the lake primarily for migration, and do not appear to have significant trophic interactions with the lake system. The introduction of hybrid bass was not depicted in the models, since it was for the most part sterile, it did not contribute to system feedback. Its effect on the system is equivalent to assessing isolated negative input to its prey, which is primarily mysid shrimp and bluegill (Gestring 1991). The reintroduction of yellow perch also was not modeled, as their populations appear to remain at very low levels, and likely do not have a significant affect on trophic dynamics in the lake system.

Where trophic relationships were uncertain, alternate models were constructed to judge the robustness of the results. Assertions of results presented in the follow 6 models were supported by all alternate models; in the following analysis we briefly describe each model, its predictions, and explain management implications.

Model 1, the pre-1920's native community

The native community of Tenmile Lake depicted in Model 1 (Figure 7) consisted of four resident fish species, with cutthroat trout as a top predator. In this model, and all subsequent models, juvenile coho salmon are depicted as being self-regulated, owing to the contribution of production from outside the model system during the stream and ocean phases of their life cycle. Basal species are also self-regulated, which accounts for their role as primary consumers. This model was stable, and had a relatively high amount of negative feedback. The prediction matrix for this model (Table 2) shows positive input to any one species in the system to produced a positive response in the population of that species. These self-responses are viewed along the diagonal trace of the prediction matrix. In this system coho salmon and cutthroat trout appear to be negatively correlated in terms of their response to changes in the system. To observe this negative correlation, note the responses in their respective columns of the prediction matrix; they are of opposite sign in 10 out of 13 rows. This suggests that when populations of coho salmon were at a relative high, cutthroat trout would usually have been at a relative low. Also note that coho salmon in this model would have been responsive to direct management input to itself, or by input to the food web.

Model 2, the 1920-1963 community

Model 2 depicts the introduction of yellow perch and brown bullhead (Figure 8). While this model was stable, the fate of coho salmon in the system was dramatically altered. Note that for coho salmon an increase in their birth rate is predicted to elicit no change in their population size, and a positive increase in their predator the yellow perch (Table 3). Coho salmon in this model appear to be largely isolated from input to the system, with most of their population responses being nil. Neutral responses are predicted for coho salmon to all increases in their food except for mysid shrimp. To observe this examine the response of coho salmon in columns associated with AM, EP, DI, CP, and OD in Figure 8. This suggests that for coho salmon in Model 2, increases in production from an increased food supply would be passed on to their predator, the yellow perch, with no net gain for coho salmon. Thus with the first introduction of exotic species in the system, direct management control of coho salmon was lost.

In Model 2 the system as a whole appears to have been less responsive to input. Every row, except those for mysid shrimp and prickly sculpin contain neutral responses; in Model 1, only five rows exhibited neutral responses. In Model 2 responses by coho salmon and cutthroat trout are either neutrally, or positively correlated with each other, but not negatively correlated as they primarily were in Model 1 of the native community model.

Model 3, the 1964-1968 community

Model 3, which is stable, illustrates the unauthorized introduction of bluegill (Figure 9, Table 4). The addition of bluegill to the community appeared to restore the responsiveness of the system, in contrast to Model 2. The community is this configuration predicted the direct management control of coho salmon; and an increases to the population of coho salmon resulting from inputs to their food base. This model is similar to Model 1 of the native community, in that coho salmon exhibit no neutral response to any input to the system, but it differs from Model 1 in that coho salmon and cutthroat trout show a more equal mix of positively and negatively correlated responses to each other as affected by input to the system.

Model 4, the 1969-1970 community

Model 4 (Figure 10) , which is stable, depicts the rotenone removal of yellow perch, and the persistence of brown bullhead, bluegill, and all native species. Historically it is a trivial model, as it represents only 2 years of the system. But it is noteworthy that the prediction matrix (Table 5) for coho salmon, and the system as a whole, is again filled with neutral responses as in Model 2, and therefore the community would have been less responsive to management in this configuration.

Model 5, the 1971-1993 community

Model 5 (Figure 11), which is stable, illustrates the purposeful introduction of largemouth bass and hybrid bass to control an overpopulation of blue gill. While largemouth bass are widely employed as a means of controlling bluegill populations elsewhere, model 5 predicts the opposite effect for the Tenmile Lakes fish community. Increases to largemouth bass effect an increase in the bluegill populations (i.e. see bottom row of Table 6 for column associated with BG for bluegill). The effect of hybrid bass in Model 5 can be interpreted as negative input to its prey mysid shrimp and bluegill. To determine the effects of negative input in a prediction matrix, the sign of the responses are reversed. In Table 6, a negative input to the two prey species of hybrid bass (mysid shrimp and bluegill) each predict a decrease in the population of coho salmon, which again is opposite to the desired management objectives. Similar to Models 2 and 4, Model 5 is filled with neutral responses in the prediction matrix, especially for coho salmon. In this system responses of coho salmon and cutthroat trout are either neutrally, or positively correlated with each other.

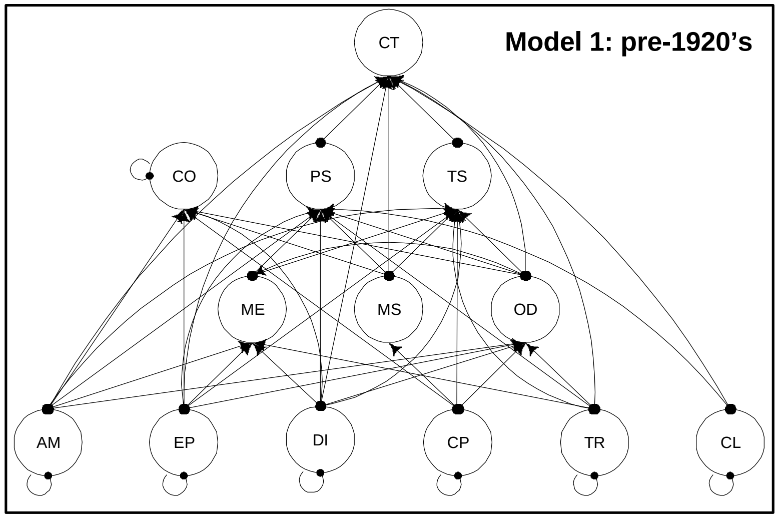


Figure 7. Signed digraph of native Tenmile Lakes fauna, circa pre-1920’s; AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, CT: cutthroat trout.

Table 2. Model 1 prediction matrix for native Tenmile Lakes fauna, circa pre-1920’s; AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, CT: cutthroat trout.

	AM	EP	DI	CP	TR	CL	ME	MS	OD	CO	PS	TS	CT
AM	1	-1	-1	1	-1	1	0	-1	1	1	1	1	-1
EP	-1	1	-1	1	-1	1	0	-1	1	1	1	1	-1
DI	-1	-1	1	1	-1	1	0	-1	1	1	1	1	-1
CP	-1	-1	-1	1	1	1	0	1	-1	1	-1	1	1
TR	1	1	1	1	1	1	1	1	-1	-1	-1	1	1
CL	-1	-1	-1	1	1	1	0	1	-1	1	1	-1	1
ME	1	1	1	1	-1	1	1	1	-1	-1	-1	1	1
MS	1	1	1	1	1	1	1	1	-1	1	-1	1	1
OD	-1	-1	-1	-1	-1	-1	-1	1	1	1	1	-1	-1
CO	-1	-1	-1	-1	1	-1	-1	-1	1	1	1	-1	-1
PS	-1	-1	-1	-1	-1	-1	-1	-1	1	1	1	-1	-1
TS	1	1	1	1	-1	1	1	1	-1	-1	-1	1	1
CT	1	1	1	1	1	1	1	1	-1	-1	-1	1	1

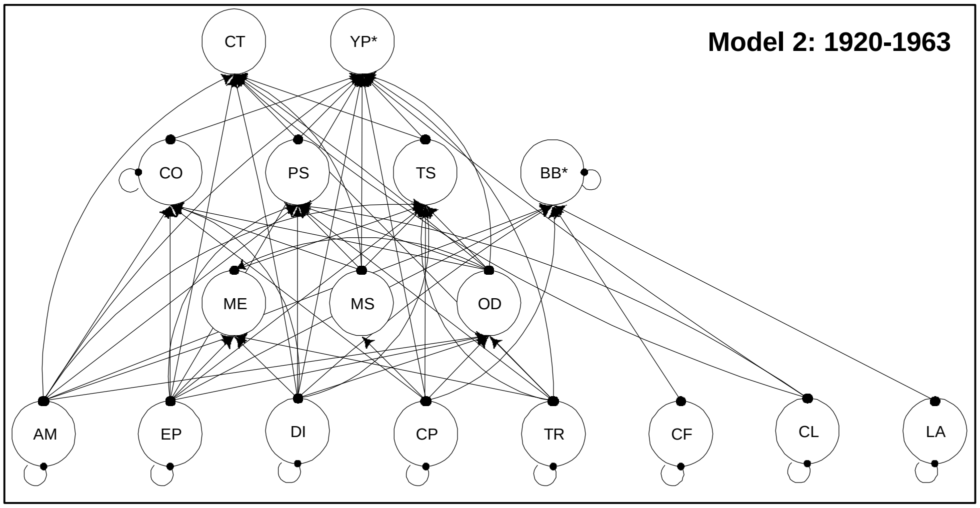


Figure 8. Signed digraph of Tenmile Lakes fauna, ca.1920-1963, with 2 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BB*: brown bullhead, CT: cutthroat trout, YP*: yellow perch.

Table 3. Model 2 prediction matrix for Tenmile Lakes fauna, ca.1920-1963, with 2 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BB*: brown bullhead, CT: cutthroat trout, YP*: yellow perch.

	AM	EP	DI	CP	TR	CF	CL	LA	ME	MS	OD	CO	PS	TS	BB*	CT	YP*
AM	1	-1	-1	0	-1	-1	1	-1	1	-1	0	0	-1	1	1	0	1
EP	-1	1	-1	0	-1	-1	1	-1	1	-1	0	0	-1	1	1	0	1
DI	-1	-1	1	0	-1	-1	1	-1	1	-1	0	0	-1	1	1	0	1
CP	0	0	0	0	0	0	0	0	0	1	0	0	-1	0	0	0	1
TR	-1	-1	-1	0	1	1	1	1	1	1	0	0	-1	1	-1	1	-1
CF	-1	-1	-1	0	1	1	-1	-1	-1	1	0	0	1	-1	1	0	-1
CL	1	1	1	0	1	-1	1	-1	1	1	-1	0	-1	-1	1	1	1
LA	-1	-1	-1	0	1	-1	-1	1	-1	1	0	0	1	-1	1	0	-1
ME	1	1	1	0	1	-1	1	-1	1	1	-1	0	-1	1	1	1	-1
MS	1	1	1	-1	1	-1	1	-1	1	1	-1	1	-1	1	1	1	-1
OD	-1	-1	-1	0	-1	1	-1	1	-1	-1	1	0	1	-1	-1	-1	-1
CO	0	0	0	0	0	0	0	0	0	-1	0	0	1	0	0	-1	1
PS	-1	-1	-1	1	-1	-1	-1	-1	-1	-1	1	-1	1	-1	1	-1	1
TS	-1	-1	-1	0	-1	1	1	1	-1	-1	1	0	0	1	-1	0	-1
BB*	-1	-1	-1	0	1	-1	-1	-1	-1	1	0	0	1	-1	1	0	-1
CT	0	0	0	0	1	0	1	0	1	1	-1	1	-1	0	0	1	-1
YP*	1	1	1	-1	-1	-1	1	-1	1	1	-1	-1	-1	1	1	0	1

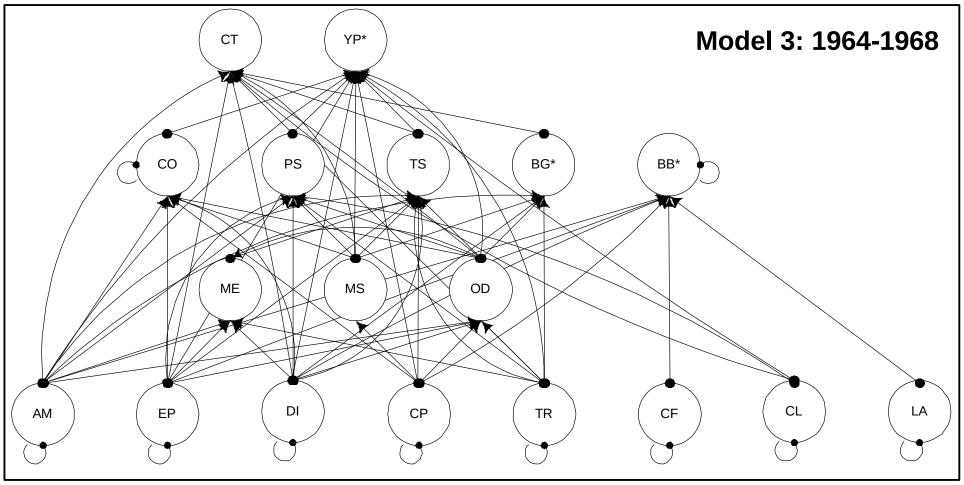


Figure 9. Signed digraph of Tenmile Lakes fauna, 1964-1968, with 3 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill, BB*: brown bullhead, CT: cutthroat trout, YP*: yellow perch.

Table 4. Model 3 prediction matrix for Tenmile Lakes fauna, 1964-1968, with 3 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill, BB*: brown bullhead, CT: cutthroat trout, YP*: yellow perch.

	AM	EP	DI	CP	TR	CF	CL	LA	ME	MS	OD	CO	PS	TS	BG*	BB*	CT	YP*
AM	1	-1	-1	1	-1	-1	1	-1	1	-1	1	1	-1	1	1	1	0	1
EP	-1	1	-1	1	-1	-1	1	-1	1	-1	1	1	-1	1	1	1	0	1
DI	-1	-1	1	1	-1	-1	1	-1	1	-1	1	1	-1	1	1	1	0	1
CP	-1	-1	-1	1	1	1	-1	1	-1	1	1	1	-1	-1	1	-1	0	1
TR	-1	-1	-1	-1	1	1	1	1	1	1	-1	-1	-1	1	-1	-1	1	-1
CF	-1	-1	-1	-1	1	1	-1	-1	1	1	-1	-1	1	1	-1	1	0	-1
CL	1	1	1	1	1	-1	1	-1	1	1	-1	1	-1	-1	1	1	1	1
LA	-1	-1	-1	-1	1	-1	-1	1	1	1	-1	-1	1	1	-1	1	0	-1
ME	1	1	1	-1	1	-1	1	-1	1	1	-1	-1	-1	1	-1	1	1	-1
MS	1	1	1	-1	1	-1	1	-1	1	1	-1	1	-1	-1	1	1	1	-1
OD	-1	-1	-1	-1	-1	1	-1	1	-1	-1	1	-1	1	-1	-1	-1	-1	-1
CO	-1	-1	-1	1	1	1	-1	1	-1	-1	1	1	1	-1	1	-1	-1	1
PS	-1	-1	-1	1	-1	-1	-1	-1	-1	-1	1	-1	1	-1	1	1	-1	1
TS	1	1	1	-1	-1	-1	1	-1	1	-1	1	-1	-1	1	-1	1	0	1
BG*	-1	-1	-1	1	1	1	-1	1	-1	1	1	1	1	-1	1	-1	0	-1
BB*	-1	-1	-1	-1	1	-1	-1	-1	1	1	-1	-1	1	1	-1	1	0	-1
CT	1	1	1	-1	1	-1	1	-1	1	1	-1	1	-1	1	-1	1	1	-1
YP*	-1	-1	-1	1	1	1	-1	1	-1	1	1	1	-1	-1	1	-1	0	1

Model 6, the 1994-1999 community

Model 6 details the unauthorized introduction of black crappie (Figure 12). This model has zero overall feedback, and as such is neutrally stable. Reliable prediction matrices cannot be developed for neutrally stable systems. Such systems can be characterized by having no response to input, and are essentially unmanageable through the biota of the system. System behavior is chaotic, and unpredictable. Recovery time from disturbances can be uncommonly long, and likely longer than the typical return time of the natural disturbance regime. Input to the system is not desirable. In the least, input will not produce consistent long term results, or at worst it could induce large fluctuations that propagate through a long time series, and produce unpredictable and unintended consequences.

Consequences of introduced exotics

Inspection of the prediction matrix for Models 1 through 5 indicate that the native community, free from exotics, was the most manageable system. Positive input to a species uniformly produced increases in the abundance of that species; and vice versa, a negative input induced decreased abundance. Management of this system could have proceeded directly through the biota. Increases in the birth rate of coho salmon, for instance via a hatchery program, or decreases in death rate, via harvest regulation, was predicted to have elicited the desired effect of an increased population. With the introduction of brown bullhead and yellow perch in Model 2, direct input to coho salmon produced no effect, and thus direct management of coho salmon was lost. Introduction of bluegill in Model 3 reestablished positive response in coho salmon to input, but subsequent Models 4 and 5, which detail the removal of yellow perch, and the introduction of largemouth bass, show coho salmon to be unresponsive to system input. Through the general history of in fish introductions in the Tenmile Lakes system, coho salmon generally exhibit a loss of responsiveness to system input.

This modeling exercise suggests that the introduction of exotic fishes can alter the relationships between native species, as was exhibited by the inverted patterns of correlation between coho salmon and cutthroat trout. It also calls into question commonly accepted beliefs regarding the generality of some predator-prey relationships. While the ability of largemouth bass to control bluegill is routinely employed as a management tool in the communities in which these fish are native, when introduced into a “foreign” community, unexpected indirect effects can be promulgated through complex webs of interactions, and produce results that are directly opposite to those intended.

This historical analysis of Tenmile Lakes imparts immediacy to Stephen Forbes’ century old imperative to consider the whole system, and makes clear the need for managers to think explicitly about the consequences of system feedback when considering actions that alter community structure. The behavior of trophic systems can be counterintuitive to traditional notions based solely on direct effects, when in fact indirect effects, acting through the foodchain, can be more important. Experience gained from introductions in other systems (Li and Moyle 1993), has often shown exotic species to invoke such novel and intense interactions that system stability is compromised, and ensuing extinctions cause a loss of biodiversity (Zaret and Paine 1973, Hughes 1986, Spencer et al. 1991). Tenmile Lakes presents a somewhat different experience, with not a loss of species diversity, but rather a loss of management options and control. The lessons being that 1) introduction of a species can, through indirect effects, change the relationships between other species, and nullify or reverse the results of management actions in the system. 2) The ability of a predator to control a prey population is dependent on the structure of the community in which they occur. 3) As more species are added to a community, the system becomes less responsive to input, and target species can become isolated from direct control. 4) When introductions are taken to an extreme, system feedback can become so weak (neutrally stable) that the entire system does not respond to input at all.

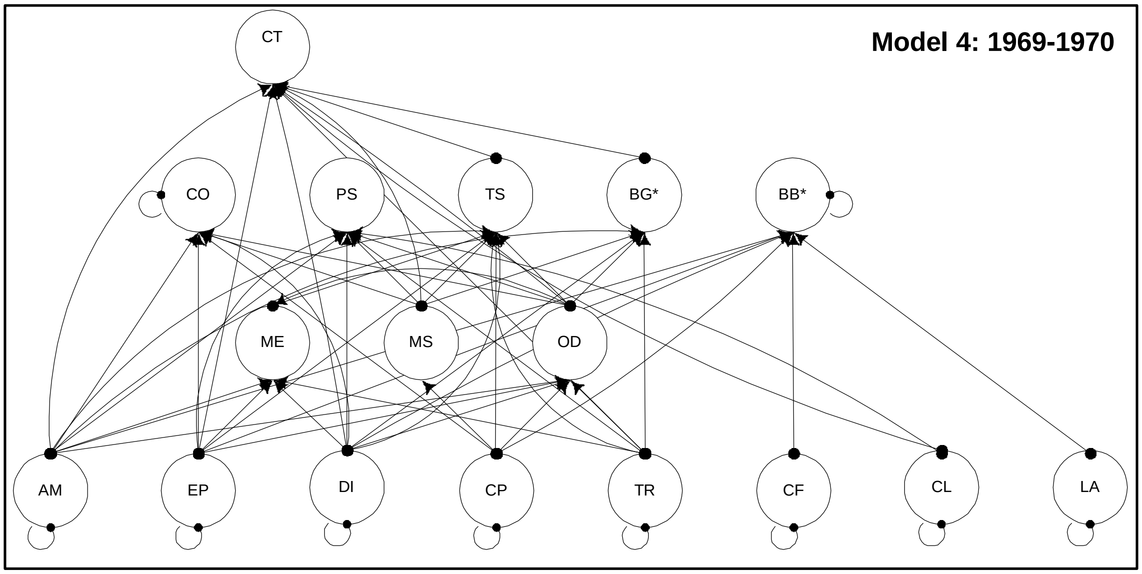


Figure 10. Signed digraph of Tenmile Lakes fauna, 1969-1970, with 2 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill, BB*: brown bullhead, CT: cutthroat trout.

Table 5. Model 4 prediction matrix for Tenmile Lakes fauna, 1969-1970, with 2 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill, BB*: brown bullhead, CT: cutthroat trout.

	AM	EP	DI	CP	TR	CF	CL	LA	ME	MS	OD	CO	PS	TS	BG*	BB*	CT
AM	1	-1	-1	0	-1	-1	1	-1	1	-1	0	0	-1	1	-1	1	0
EP	-1	1	-1	0	-1	-1	1	-1	1	-1	0	0	-1	1	-1	1	0
DI	-1	-1	1	0	-1	-1	1	-1	1	-1	0	0	-1	1	-1	1	0
CP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-1	0	0
TR	-1	-1	-1	0	1	1	1	1	1	1	0	0	-1	-1	1	-1	1
CF	-1	-1	-1	0	1	1	-1	-1	-1	1	0	0	1	-1	1	1	0
CL	1	1	1	0	1	-1	1	-1	1	1	-1	0	-1	1	-1	1	1
LA	-1	-1	-1	0	1	-1	-1	1	-1	1	0	0	1	-1	1	1	0
ME	1	1	1	0	1	-1	1	-1	1	1	-1	0	-1	1	1	1	1
MS	0	0	0	0	1	0	0	0	0	1	-1	1	-1	-1	1	0	1
OD	-1	-1	-1	0	-1	1	-1	1	-1	-1	1	0	1	-1	1	-1	-1
CO	0	0	0	0	0	0	0	0	0	-1	0	0	1	1	-1	0	-1
PS	1	1	1	0	-1	-1	-1	-1	-1	-1	0	-1	1	1	-1	1	-1
TS	1	1	1	-1	-1	-1	1	-1	1	-1	0	-1	-1	1	-1	1	0
BG*	-1	-1	-1	1	1	1	-1	1	-1	1	1	1	1	-1	1	-1	0
BB*	-1	-1	-1	0	1	-1	-1	-1	-1	1	0	0	1	-1	1	1	0
CT	0	0	0	0	1	0	1	0	1	1	-1	1	-1	-1	1	0	1

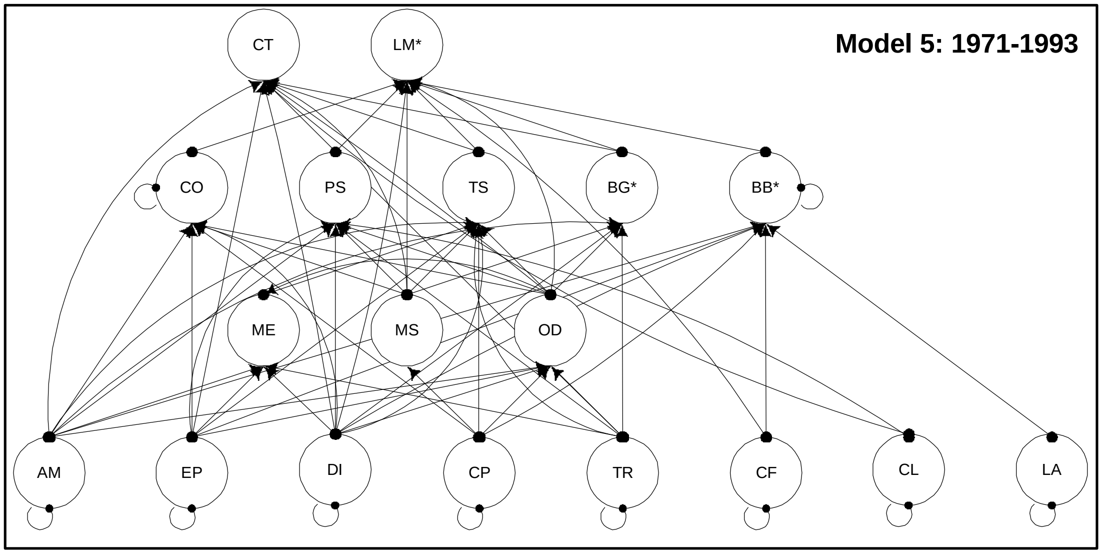


Figure 11. Signed digraph of Tenmile Lakes fauna, 1971-1993, with 3 introduced species; AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill , BB*: brown bullhead, CT: cutthroat trout, LM*: largemouth bass.

Table 6. Model 5 prediction matrix for Tenmile Lakes fauna, 1971-1993, with 3 introduced species; AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill, BB*: brown bullhead, CT: cutthroat trout, LM*: largemouth bass.

	AM	EP	DI	CP	TR	CF	CL	LA	ME	MS	OD	CO	PS	TS	BG*	BB*	CT	LM*
AM	1	-1	-1	0	-1	-1	-1	-1	-1	-1	1	0	1	1	-1	1	-1	-1
EP	-1	1	-1	0	-1	-1	-1	-1	-1	-1	1	0	1	1	-1	1	-1	-1
DI	-1	-1	1	0	-1	-1	1	-1	1	-1	-1	0	-1	1	-1	1	1	1
CP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-1	0	0	0
TR	-1	-1	-1	0	1	1	1	1	1	1	1	0	-1	-1	1	-1	1	-1
CF	1	1	-1	0	1	1	1	-1	1	1	-1	0	-1	-1	1	1	1	1
CL	-1	-1	1	0	1	1	1	-1	1	1	-1	0	1	1	-1	1	1	-1
LA	-1	-1	-1	0	1	-1	-1	1	-1	1	-1	0	-1	-1	1	1	1	1
ME	-1	-1	1	0	1	1	1	-1	1	1	-1	0	-1	1	1	1	1	-1
MS	0	0	0	0	1	0	0	0	0	1	-1	1	-1	-1	1	0	1	0
OD	-1	-1	-1	0	-1	1	1	1	1	1	1	0	1	-1	1	-1	-1	1
CO	0	0	0	0	0	0	0	0	0	-1	0	0	1	1	-1	0	-1	0
PS	1	1	1	0	-1	-1	-1	-1	-1	-1	-1	-1	1	1	-1	1	-1	1
TS	1	1	1	-1	-1	1	-1	-1	-1	-1	1	-1	1	1	-1	1	-1	-1
BG*	-1	-1	-1	1	1	-1	1	1	-1	1	1	1	-1	-1	1	-1	1	1
BB*	-1	-1	-1	0	1	-1	-1	-1	-1	1	-1	0	-1	-1	1	1	1	1
CT	-1	-1	1	0	1	1	1	-1	1	1	-1	1	-1	-1	1	1	1	-1
LM*	1	1	-1	0	1	-1	1	1	1	1	-1	0	-1	1	1	-1	1	1

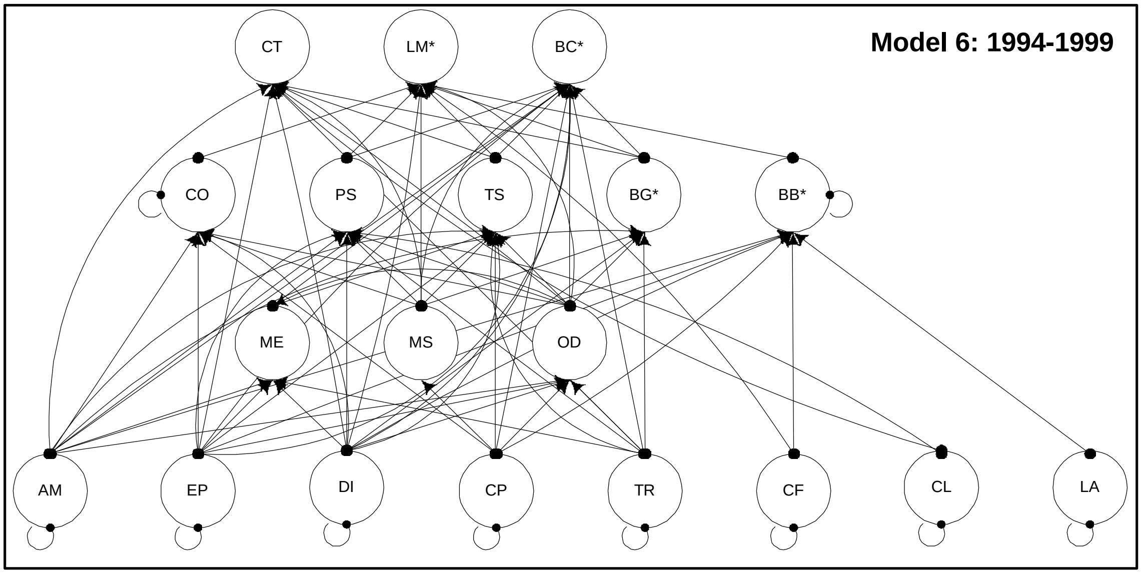


Figure 12. Signed digraph of Tenmile Lakes fauna, 1994-1999, with 4 introduced species (*); AM: amphipod, EP: Ephemeroptera, DI: Diptera, CO: copepod, TR: Tricoptera, CF: crayfish, CL: clam, LA: lamprey ammocoetes, ME: Megaloptera, MS: mysid shrimp, OD: Odonata, CO: coho salmon parr, PS: prickly sculpin, TS: threespine stickleback, BG*: bluegill , BB*: brown bullhead, CT: cutthroat trout, LM*: largemouth bass, BC* black crappie.

Utility of qualitative modeling

While a historical approach was employed in this study, qualitative modeling can also be used to complement ongoing research and management programs, and to pose and test competing hypotheses regarding the stability or behavior of natural systems. In systems where community structure is uncertain, it can be employed in a heuristic manner to quickly develop testable hypotheses, and to direct research questions for adaptive management. The construction of alternate models and comparison of prediction matrices can be used to assess the robustness of model results, and weigh the risks associated with alternate management options.

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